

The Relevance of Phylogenetic Systematics to Biology: Examples from Medicine and Behavioral Ecology

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ABSTRACT

Results of phylogenetic analysis are frequently used to investigate the pattern of evolution of characteristics of interest. In examples such as the evolution of spider webs, the number of horns on a rhinoceros or social behavior in halictine bees, the results of phylogenetic tests may lead to traditional views being overturned. However, conclusions based upon phylogenetic analyses of evolutionary pattern require careful consideration of character coding and taxonomic sampling as indicated by studies of rhinos and HIV respectively. Phylogenetic results are less often used to direct further research, an area of their application which remains underutilized. In this paper I concentrate on the application of phylogenetics to problems of social evolution in halictine bees. There are seven genera/subgenera that are known to contain both solitary and social species and at least 9 species which exhibit behavioral polymorphism with both solitary behavior and eusociality found within the same or different populations. *A priori*, these taxa would seem to be the best ones to use in tests of the selective advantages of eusociality. However, results of phylogenetic analysis indicate that in the majority of cases (*Halictus*, *Seladonia*, *Augochlorella* and *Augochlora*) it is solitary behavior that is the recent evolutionary innovation and eusociality is ancestral. Use of the non-phylogenetic approach to the comparative method in each of these instances would not provide information on origins of eusociality. In contrast, eusociality appears to be derived in both the subgenera *Lasioglossum* (in the species *L. aegyptiellum* for which the limited field-collected data are presented for the first time) and *Evylaeus*. Overall, of the nine species for which both eusociality and solitary behavior have been recorded, solitary behavior is the recent acquisition in at least 6 cases, and the only probable case of recent origin of eusociality exhibited by behaviorally polymorphic species (*Lasioglossum (Evylaeus) comagenense* and *L. (E.) fratellum*) refers to origin of delayed eusociality. The application of phylogenetic methods to the study of evolutionary pattern suggests both which taxa are deserving of further field work and which require additional phylogenetic analysis.

RÉSUMÉ

L'intérêt de la systématique phylogénétique pour la biologie : quelques exemples issus de la biologie médicale et l'éco-éthologie

Les résultats des analyses phylogénétiques sont fréquemment utilisés pour inférer les séquences d'évolution de caractères d'intérêt particulier. Dans des exemples tels que l'évolution des toiles d'araignées, du nombre des cornes de rhinocéros, ou du comportement social des abeilles halictes, les résultats des tests phylogénétiques peuvent conduire à réfuter des schémas traditionnels d'évolution. Cependant, les conclusions basées sur l'analyse phylogénétique des séquences évolutives sont dépendantes du codage des caractères et d'un échantillonnage taxonomique suffisant, comme cela est montré à propos des études concernant les rhinocéros et le virus HIV. Les résultats phylogénétiques peuvent être aussi utilisés pour orienter de futures recherches, ce qui constitue un domaine de recherche encore trop peu exploré. Cette article concerne principalement

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l'application de la systématique phylogénétique aux problèmes d'évolution sociale chez les Abeilles Halictes. Il y a sept genres/sous-genres qui sont connus pour regrouper non seulement des espèces solitaires et des espèces sociales mais aussi au moins neuf espèces dont le polymorphisme comportemental englobe des comportements solitaires et eusociaux trouvés dans les mêmes populations ou dans des populations différentes. *A priori*, ces taxa devraient donc parfaitement convenir au test des avantages que conférerait l'eusocialité en regard de la sélection naturelle. Cependant, les résultats de l'analyse phylogénétique indiquent que dans la majorité des cas (*Halictus*, *Seladonia*, *Augochlorella* et *Augochlora*), c'est le comportement solitaire qui est l'innovation évolutive et l'eusocialité qui est ancestrale. Dans chacun de ces cas, une approche non-phylogénétique de biologie comparative n'aurait pas fourni d'information sur les origines de l'eusocialité. L'approche phylogénétique indique que l'eusocialité est dérivée à la fois dans deux des sous-genres de *Lasioglossum* (chez l'espèce *L. aegyptiellum* pour qui des données de terrain sont présentées ici pour la première fois) et dans le genre *Evyllaes*. Globalement, des neufs espèces chez qui l'eusocialité et le comportement solitaire ont été tous deux rapportés, le comportement solitaire est l'acquisition récente dans au moins six cas. Le seul cas probable d'origine récente de l'eusocialité chez des espèces au comportement polymorphique (*Lasioglossum (Evyllaes) comagenense* et *L. (E.) fratellum*) concerne une origine de l'eusocialité différée. L'application de la méthode phylogénétique à l'étude de l'évolution permet de déterminer à la fois quels taxa requièrent des études de terrain et quels taxa nécessitent des études phylogénétiques supplémentaires.

INTRODUCTION

In this paper I wish to explore the utility of phylogenetic systematics in providing answers to two questions: i) what are we studying? and ii) what should we be studying? It may seem that answers to these questions are self evident – surely we always know what it is that we are investigating and are always confident that this is indeed what we should be studying. However, recent reanalyses indicate that the confidence with which we approach our studies is often misplaced.

What are we studying?

When biologists make comparisons of some feature of interest which varies between taxa we generally rely upon “common sense” arguments as to the adaptive value of the differences we observe. Species A has some condition which is a result of adaptation to its environment whereas species B has some other state which is similarly adaptive. We study how both characteristics function in their respective species/environments and understand both states to be adaptive. However, the minimal requirement for a characteristic to be considered to be an adaptation is that it is a derived feature (CODDINGTON, 1988, 1995; GRANDCOLAS *et al.*, 1994; CARPENTER, 1997, this volume). In comparing states between the species one of them is likely ancestral to the other. It is the evolutionary change between states that represents the results of selection and hence provides evidence for adaptation. Consequently, we need to know the polarity of evolutionary change between character states; only then will we know what the direction of evolutionary change in the character of interest has been: *i.e.*, only then will we really know what it is that we are studying.

Results of phylogenetic analysis indicate that common sense approaches to polarity are often wrong. For example, consider spider webs of the cob and orb varieties. It is common sense to suggest that the rather untidy cobwebs made by some spiders served as an antecedent to orb webs, after all, they are apparently simpler in design and are constructed in places where it seems easier for spiders to negotiate web building. However, phylogenetic analysis demonstrates the reverse to be true: the orb web is ancestral to cobwebs with the latter arising several times independently in different spider lineages (CODDINGTON, 1988). Thus, in comparing cob and orb webs we would be answering questions about the selective advantage of cob versus orb webs

whereas the common sense, non-phylogenetic, approach suggests we would be looking at the converse – the benefits of orb over cob webs.

Another classic example, the evolution of horn number in rhinoceroses, has recently become more complex and illustrates the importance of careful character coding (DELEPORTE, 1993). A “common sense” argument is that as i) the protorhino condition would have zero as the number of horns along the midline of the head and ii) rhinos come with one or two horns, then the evolution of horn number must have followed the mathematically simple sequence of 0, to 1, to 2. However, a morphological phylogeny (GROVES, 1983) indicated unambiguously that one horned rhinos have evolved from 2 horned ancestors (CODDINGTON, 1988). Conversely, a recent molecular phylogeny (MORALES & MELNICK, 1994) is consistent with the 0 to 1 to 2 scenario in that one-horned rhinos form the first branch in the ingroup. Combined data in a total evidence analysis (PACKER, unpublished) leads to various possible interpretations of evolutionary change in this character depending upon how horn number is coded. If treated as an ordered character then there are two equally parsimonious resolutions of horn number evolution: i) from 0 to 2 (through 1) in the common ancestor, with a reduction to one horn in *Rhinoceros* (Fig. 1A) or ii) from 0 to 1 in the ancestor followed by a change from 1 to 2 horns on two separate occasions (Fig. 1B). As an unordered character, 0 to 2 to 1 is the single most parsimonious result (Fig. 1A). This illustrates the problems that can arise as a result of alternative coding methods for the characteristics of interest, a point that will be returned to later. However inclusion of fossil genera demonstrates clearly that among extant rhinoceros, loss of the frontal horn has occurred and so the polarity of change in horn number among extant rhinos is indeed from 2 to 1 (PACKER, unpublished).

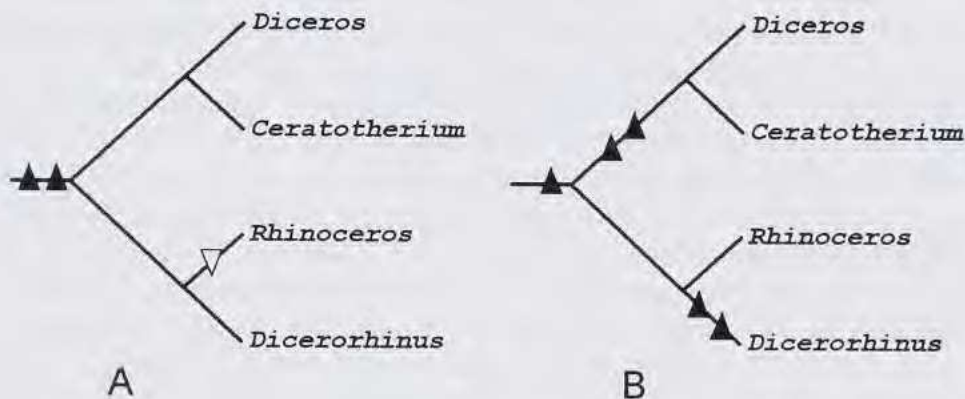


FIG. 1. — Evolution of horn number in extant rhinoceros. A: If treated as an unordered character then two evolutionary changes are required - from 0 to 2 in the ancestor and from 2 to 1 in *Rhinoceros*. If treated as an ordered character, then three changes are required, from 0 to 2 (through 1) in the common ancestor and from 2 to 1 in *Rhinoceros* or B: from 0 to 1 in the ancestor with two independent derivations of the second horn.

In much of modern evolutionary biology “common sense” is replaced by more complex models based upon population genetics or evolutionary ecology. However, scenarios predicted

by these sophisticated approaches can also be shown to be false using phylogenetic methods (ANDERSEN, 1997, this volume).

Although these examples stand out because their conclusions are counterintuitive, it is precisely this point that I wish to make - in the absence of a phylogenetic test of some *a priori* notion, one is likely to make mistakes by relying upon common sense biological "knowledge". These mistakes may lead to researchers spending a considerable amount of time (and money) asking the wrong question; a research program aimed at answering the question "what selection pressures caused the evolution of orb webs from cob webs?" would, at best, be doomed to inadequacy from the outset. For excellent accounts of the use of phylogenetic approaches and definitions and tests of adaptation see GRANDCOLAS *et al.* (1994) and CODDINGTON (1995).

What should we be studying?

Whereas mapping characters onto a phylogeny to verify or refute a scenario is becoming de rigueur in evolutionary biology (see most of the papers in this volume), the use of a cladogram to direct future research seems underutilized. Not only does phylogenetic analysis permit us to know the polarity of evolutionary change between character states, it also locates the position of the transition between states on the phylogeny. Clearly, comparisons of taxa on either side and in close proximity to this juncture are most likely to provide clues as to causation. These are the organisms that we should be studying; the comparisons that can most fruitfully be made.

The trouble is that our information is rarely complete. Phylogenetic studies of characteristics of interest usually cannot include all taxa because not all species are known for the traits of interest, phylogenetic information is incomplete, or both. There are several ways to overcome these limitations.

It may be possible to make an educated guess as to the state of some character of interest if a species is unknown behaviorally or ecologically but its position phylogenetically is known. For example, BROOKS *et al.* (1992) used phylogenetic analysis as a guide to field research and as a result discovered the breeding site of *Etheostoma wapiti*, an endangered fish species whose habitat requirements were not known. It is probable that discovery of the breeding site requirements of this species would have been delayed if it weren't for the application of phylogenetics to this problem. Thus, phylogenetic results can be used to guide field work.

Another approach is to produce a phylogeny for those species for which data of interest are available. With a phylogeny based upon a restricted sample of taxa it is still possible to trace the approximate position of a character state change of interest. Further systematic research can then add taxa to the phylogeny, concentrating upon those species thought to lie close to the transition point in the phylogeny. The results of this second phylogenetic iteration may then be used as a guide to which species should be the subjects of field research. This procedure greatly simplifies the problem of phylogenetic reconstruction, especially for speciose groups, although there is some potential for loss of accuracy when large proportions of a group are left out of a phylogenetic analysis. A more insidious cause of potential error with this approach is biased sampling of taxa. Consider some character state to be of great interest in comparison to the alternative condition: it is more likely that information on species possessing the interesting condition will be reported than data on the absence of the feature of interest. Species within higher level taxonomic groups will then have an unrealistic preponderance of the interesting condition and the results of mapping character traits onto the phylogeny will be biased in favor of

optimizing the interesting character state as ancestral. I will return later to an example of this in bees, but will first turn to a medical example.

The Evolution of HIV

I will illustrate my point with reference to the evolution of HIV both because of the clear alternatives suggested by a phylogenetic approach and because it does serve as a great example for use in the classroom – never will a class being taught the rudiments of phylogenetic methodology be so attentive as when the evolution of HIV is being considered.

The classic story, that may be read in medical texts, is that HIV1 and HIV2 spread from non-human primates into the human population in Africa at some comparatively recent point in time and that they did this independently of each other yet more or less simultaneously (*e.g.* MYERS *et al.*, 1993), this pattern is referred to as the simian hypothesis. Figure 2A shows a phylogeny consistent with dual transfer to humans. The assumption that this disease is recent in humans is supported by the classic epidemiological dogma that diseases evolve from levels of high virulence to more benign relationships with their hosts. The high virulence of HIV (HIV1 at least) is taken by many as being the result of relatively recent introduction of the virus into human populations by cross-species infection. Combine several *a priori* notions into one logical argument and it is not likely that one will meet much opposition. Fortunately, some researchers step aside from these assumptions and test the logical bases upon which they rest. Here I will concentrate upon the potential role that different taxonomic sampling protocols may have played in this story. For details concerning the history of other criticisms of the standard dogma over HIV see GRMEK (1990).

MINDELL *et al.* (1995) have published a phylogenetic analysis of immunodeficiency viruses based upon sequence data (Fig. 2B). The most parsimonious mapping of hosts onto the viral phylogeny suggests that the common ancestor of HIV1 and HIV2 was a virus that infected human beings and that, in addition to an initial colonization event into humans, there have been multiple independent interspecies transfers from human beings to other primates. This suggests that HIV has had humans as hosts for at least several hundred years and that something other than a recent transfer into the human population is responsible for the extreme virulence of HIV1 (EWALD, 1994; MASSAD, 1996).

It is evident that analyses that leave out much of the diversity found within HIV1 and HIV2 are likely to bias the results in favor of the simian hypothesis. MINDELL *et al.* (1995) took into consideration a great diversity of HIV and SIV lineages in comparison to previous analyses (*e.g.* MYERS *et al.*, 1993). If one were to remove all but one of the HIV1 strains and all but two of the HIV2 strains from Figure 2B, using the same phylogenetic mapping logic, one would conclude that the common ancestor of HIV1 and HIV2 did indeed occur in a non-human primate and the simian hypothesis would thereby garner support simply as a result of biased sampling! This is precisely the taxon sampling protocol used by MYERS *et al.* (1993).

The currently available analyses do not suggest that a stable phylogenetic pattern for HIV/SIV evolution and evolutionary changes in host use has not been attained by HIV researchers. Nonetheless, it is clear that when a wide range of taxa are available, choice among them will influence the phylogenetic results obtained.

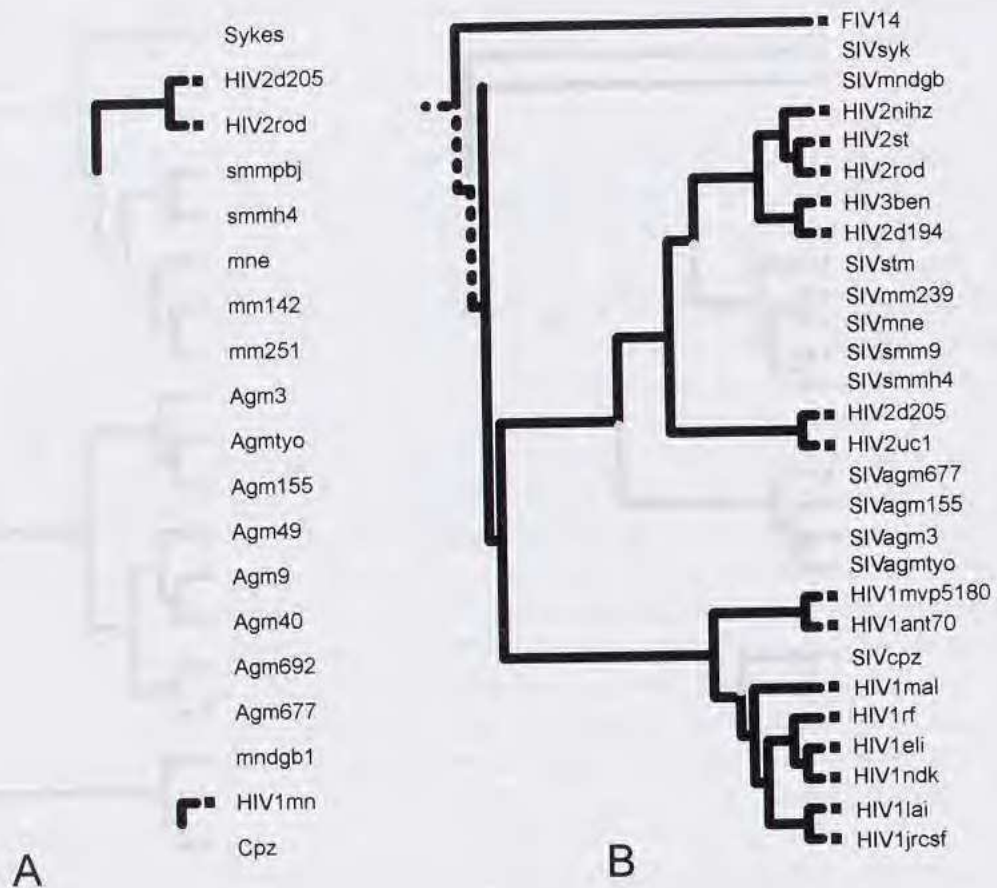


FIG. 2. — Two scenarios for the evolution of host association for primate immunodeficiency viruses. Pale grey patterns represent non-human primates as hosts, black ones refer to human hosts, dark grey ones represent feline immunodeficiency virus and dashed patterns represents ambiguous resolution. **A:** the simian hypothesis is supported by MYERS *et al.* (1993) who used only two strains of HIV2 and one of HIV1 in their analysis. **B:** a human ancestral host, a more ancient ancestry and multiple infection into non-human primates are suggested by MINDELL *et al.* (1995). Note that in both phylogenies different non-human primate hosts are not differentiated in cladogram shading. Phylogenies redrawn from both sources.

THE EVOLUTION OF SOCIAL BEHAVIOR IN HALICTINE BEES

Eusociality involves a reproductive division of labor between generations, archetypally between a mother queen and her worker daughters (WILSON, 1971; MICHENER, 1974). Among the Hymenoptera it is found in ants, vespid and sphecid wasps and various groups of bees.

There have been many theoretical treatments aimed at explaining the origins of worker sterility (partial or complete) of which the kin selection (or haplodiploidy) hypothesis has received the most attention. A fundamental prediction of this hypothesis is that female nestmate relatedness be high. But, most analyses indicate this not to be the case (GADAGKAR, 1991). However, the vast majority of tests have concerned ants and vespine wasps, taxa which have been eusocial since the Cretaceous (BRANDAO *et al.*, 1989; WENZEL, 1990). Testing a hypothesis

of origins of eusociality with these organisms is then somewhat too late, approximately 100 million generations too late. Consequently, it has been stated that halictine bees are more suitable candidates for testing hypotheses of eusocial origins (PACKER, 1991; PACKER & OWEN, 1994). One reason for this is that all halictines exhibit primitive eusociality (*i.e.* they lack a marked morphological disparity between the castes) and with few exceptions (PLATEAUX-QUÉNU, 1959; SAKAGAMI & PACKER, 1994), their societies are annual. Another reason for such optimism is the spotty taxonomic distribution of eusociality among the Halictinae. Not only are there seven genera/subgenera that contain both solitary and eusocial species (Table 1), there are at least 9 species which are known to have both solitary and social behavior as a behavioral polymorphism

TABLE 1. — Genera and subgenera of halictines which contain solitary and eusocial species. Species which are both eusocial and solitary are listed under both categories. Data from a variety of sources including YANEGA (1997) and MOURE & HURD (1987).

Genus / subgenus	Number of species		
	solitary	eusocial	unstudied
<i>Halictus</i>	4	11	80
<i>Seladonia</i>	3	8	>30
<i>Lasioglossum</i>	6	1	>60
<i>Evyllaes</i>	5	11	>60
<i>Dialictus</i>	many	many	100s
<i>Augochlorella</i>	1	3	13

TABLE 2. — List of halictine species known to exhibit behavioral polymorphism either in the same, or different population. *: delayed eusociality and the normal annual eusocial colonies have both been reported. **: eusociality known only as delayed eusociality.

<i>Halictus rubicundus</i>	different	YANEGA (1997); EICKWORT <i>et al.</i> (in press)
<i>Seladonia confusus</i>	same	TUCKERMAN (pers. com.)
<i>Seladonia tumulorum</i>	same?	STOCKHERT (1933); SAKAGAMI & EBMER (1979)
<i>Evyllaes calceatum</i> *	different	SAKAGAMI & MUNAKATA (1972)
<i>E. albipes</i> *	different	PLATEAUX-QUÉNU (1993)
<i>E. fratellum</i> **	same	VON DER HEIDE (1992); FIELD (1996)
<i>E. comagenense</i> **	same	PACKER (unpubl. obs.)
<i>Dialictus problematicum</i> **	same	SAKAGAMI & PACKER (1994)
<i>Augochlorella striata</i>	same	PACKER (1991)

(Table 2). By behavioral polymorphism I refer to a situation in which more than one type of behavior is routinely found within the species/population under normal conditions, it does not refer to a situation in which accidents of mortality cause a change in social structure (for

example, if occasional early worker mortality leaves a foundress with no option but to act as a solitary female). If a population exhibits some eusocial colonies but there is a large proportion of foundresses that produce a brood with females none of which work then that would be considered an example of behavioral polymorphism. Similarly if a species has populations that are social and others that are solitary it would also be considered to be socially polymorphic. It should be noted that in no cases have these polymorphisms been unambiguously determined as having a genetic basis, although in one case bees from solitary and eusocial populations have been shown to retain their behavioral differences when reared under identical conditions (PLATEAUX-QUÉNU *et al.*, submitted).

Arguments for both the frequency and recency of eusocial origins in the Halictinae rest on the assumption that in each (or at least most) of the examples of intraspecific behavioral polymorphism or behavioral variation within a genus/subgenus, it is eusociality that is the derived condition. But for each variable taxon this common sense approach to evolutionary polarity is a hypothesis that requires testing.

Below I will outline what we know of halictine phylogeny for each of the groups that are behaviorally variable. In all cases our knowledge is doubly incomplete – no single genus or subgenus has been subjected to a thorough phylogenetic analysis involving all species and for none of them is the behavior of all species known (Table 1). Given the large number of species in each genus/subgenus, it is doubtful that either of these areas of inquiry will be completed for any taxon in the near future. Nonetheless, phylogenetic analysis can be useful in determining which taxa are likely to be most suitable for further study both in the field and phylogenetically.

Methods

I have obtained phylogenies from the literature or from my own studies. Wherever the example illustrates a point of general procedural interest, this is noted in the subheading.

All phylogenies were either verified or obtained using Hennig86 and whenever multiple equally parsimonious trees resulted, successive approximations character weighting (CARPENTER, 1988) was invoked. Inclusion of the social behavioral data in the matrix used to produce the phylogenies is not recommended in all but one case because of the difficulties associated with including polymorphic attributes (GRANDCOLAS *et al.*, 1994; DELEPORTE, 1993) in such analyses, especially when one might want to code behavioral polymorphism as an intermediate stage between solitary and social behavior (as would seem logical).

The examples

Total evidence and character coding in Halictus and Seladonia. PESENKO (1985) provided a morphology-based phylogeny of species groups (as named subgenera) of *Halictus* and RICHARDS (1994) used allozyme electrophoresis to construct a phylogeny of many of the behaviorally known species in the subgenus and also some species of the subgenus *Seladonia*. The former analysis is more complete in terms of the number of taxa included although it is now suspected that *Seladonia* (and *Vestitohalictus*) should be included within the ingroup (*Halictus*) rather than among the outgroups (PESENKO, personal communication). Clearly, behavioral data are not available for all of the included species and not even all of the species groups that PESENKO (1985) defines. Nonetheless, mapping behavioral traits (Fig. 3) onto the phylogeny

yields the conclusion that social behavior is ancestral and solitary behavior has arisen independently at least three times (PACKER, 1986).

The electrophoretic data of RICHARDS (1994) yielded two subsets of equally parsimonious trees and in both sets it is more parsimonious to treat eusociality as ancestral with solitary behavior and social behavioral polymorphism as being derived character states.

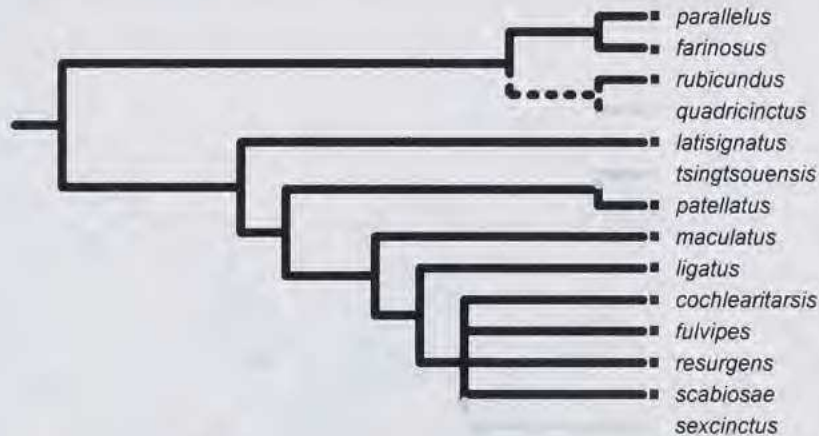


FIG. 3. — Mapping behavioral characters onto a phylogeny for *Halictus* provided by PESENKO (1985) suggests eusociality to be ancestral with multiple independent origins of solitary behavior (from PACKER, 1986). Pale grey patterns refer to solitary behavior, dark grey ones represent behavioral polymorphism and black bars indicate eusociality, dashed patterns represents ambiguity. Polymorphism coded as a third state in an unordered transformation series.

I have combined these data sets and added morphological data on *Seladonia* to produce a very preliminary “total evidence” phylogeny for the group. In the analyses presented below, the electrophoretic variables were considered as unordered and the morphological ones were ordered where possible. A smaller morphological data set than presented by PESENKO is used here as I have included only those characters whose polarity can be determined without reference to *Seladonia* as an outgroup and where character states for this subgenus could be homologized readily with those of *Halictus*. I have taken advantage of some more recent behavioral research (EICKWORT *et al.*, 1996; TUCKERMAN, personal communication) in assigning behavioral character states to terminals.

The results provided here are clearly far from complete even in terms of the representation of socially known species. Nonetheless, they do indicate the importance that choice among alternative coding schemes may have upon deduced evolutionary scenarios. Twelve equally parsimonious trees resulted from the analysis of the raw data matrix, each had a length of 159, a CI of 0.81 and RI of 0.77. One round of successive approximations character weighting led to one tree, the various statistics of which stabilized. This tree retains both subgenera *Seladonia* and *Halictus* as monophyletic groups.

Three coding methods were employed for the social behavior data: i) treating polymorphism as a third character state in an ordered transformation series ii) treating polymorphisms as a third character state in an unordered transformation series and iii) treating

polymorphic species as having eusociality. These three coding protocols suggest different phylogenetic patterns for social evolution. When polymorphism is treated as an ordered intermediary character state social polymorphism is optimized as ancestral for *Halictus* + *Seladonia* and from this, solitary behavior is lost two or three times and eusociality is lost twice (Fig. 4A). When treated as an unordered three state character with polymorphism as the third state there is still substantial ambiguity (Fig. 4B). If the presence of eusociality is coded whether

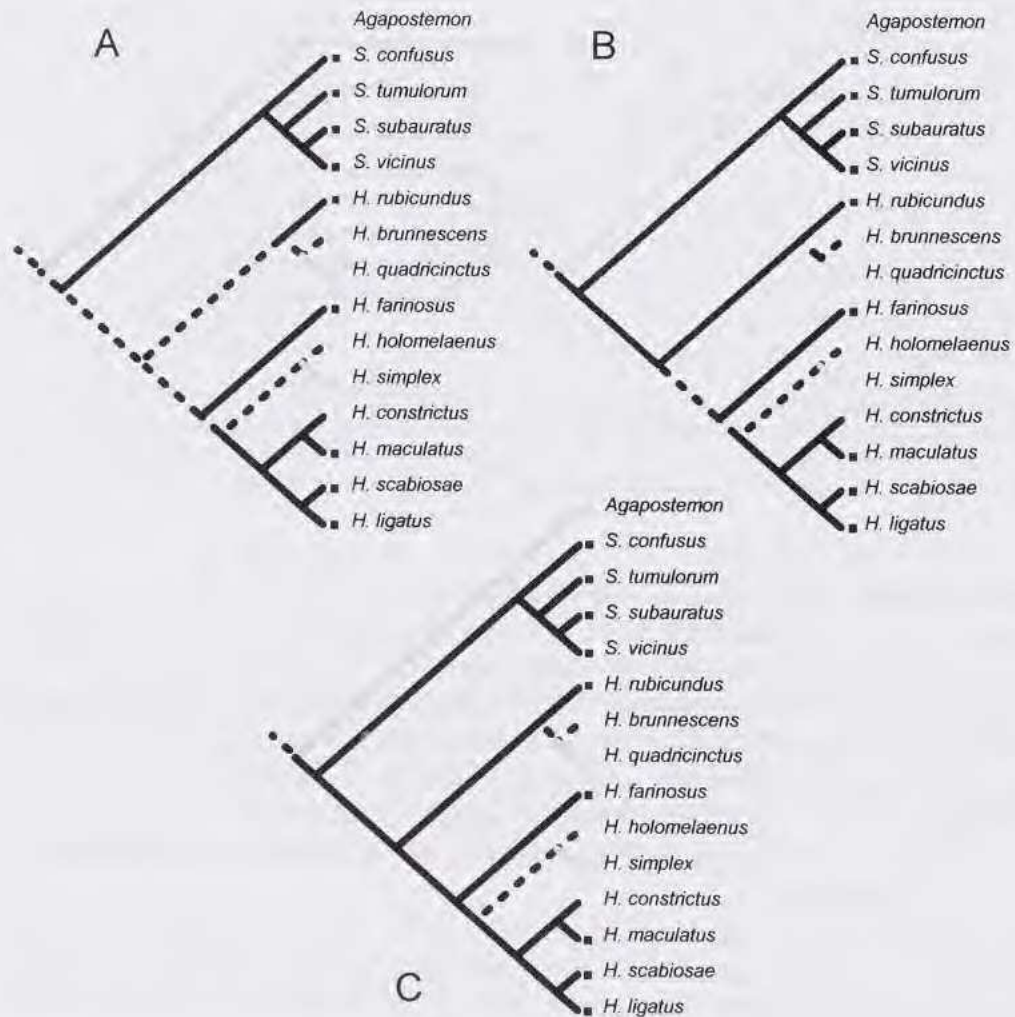


FIG. 4. — The scenarios for social evolution in *Halictus* and *Seladonia* combined with phylogenies based upon a combined data matrix from PESENKO (1985) and RICHARDS (1994). PESENKO's characters 1-6, 8-11, 17-23, 25-28, 35, 37 and 38 were included in the analysis with all multi-state characters coded as ordered except 1, 20 and 37. Note that *Agapostemon* is listed as the outgroup as this was the taxon used as such in the electrophoretic study, a much wider range of taxa were used to polarise the ingroup characters for the morphological analysis. **A:** Behavior optimized with polymorphism as a third, intermediary state. **B:** polymorphism treated as a third state in an unordered character. **C:** polymorphism treated as presence of eusociality. For explanation of cladogram shading see legend to figure 3.

polymorphic or not, then eusociality is ancestral with reversal to solitary behavior occurring at least twice (Fig. 4C).

The genus *Lasioglossum*. *Lasioglossum aegyptiellum* (Fig. 5) has been recorded as being eusocial based upon one nest excavated by KNERER. I have had the opportunity to inspect the preserved contents of this nest, although KNERER's original field notes and dissection data have been lost. The nest was excavated on August 1st, 1977 in the Camargue region of France. Five adults were found within the nest (Table 3), all had well worn wings and mandibles although the largest individual had much the greatest amount of mandibular wear and, based upon the

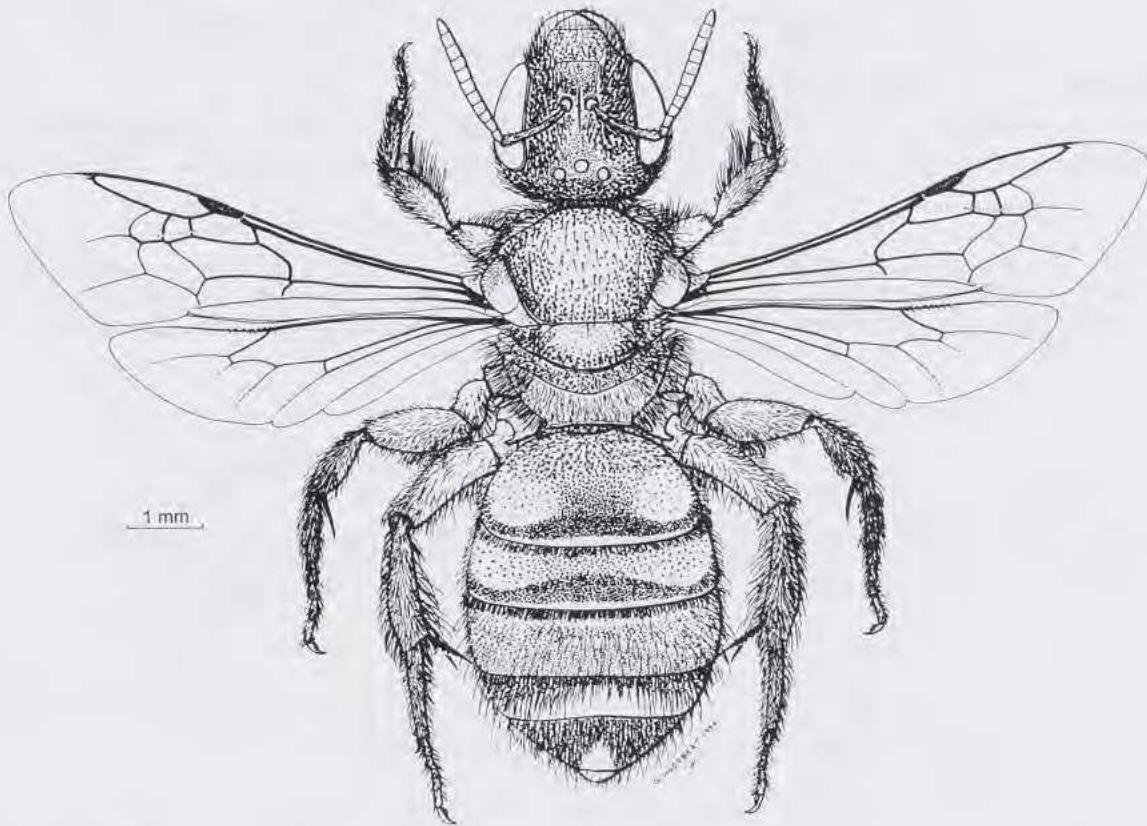


FIG. 5. — Habitus drawing of female *Lasioglossum aegyptiellum*, the species for which recent evolution of eusociality seems most readily documentable.

coloration of the wings, is the oldest individual among them, this individual is probably the queen. All individuals had well developed ovaries, although deterioration and previous dissection of the specimens makes it impossible to provide accurate ovarian development indices or to establish which among them was mated. Three male and one female pupae, five fully grown larvae and an unknown number of smaller larvae and pollen balls were also found. The female

pupa had the same head width as the largest adult female. These meager data are consistent with eusociality with poor ovarian suppression in the workers.

There is only this one species of *Lasioglossum s.str.* which may be considered to be eusocial, and at least 6 are known to be solitary (YANEGA, 1997) and so it is *a priori* probable that this represents a recent origin of eusociality (as also suggested by the high degree of ovarian development among the smaller adult females). Nonetheless, phylogenetic corroboration is needed. There are currently no phylogenies for Old World *Lasioglossum*. However, MCGINLEY (1986) has produced a phylogeny for the New World species, two of which (*leucozonium* and *zomulum*) are holarctic. *Lasioglossum aegyptiellum* belongs to the *leucozonium* group (WARNCKE, 1975; PESENKO, 1986).

I have added *L. aegyptiellum* to the phylogeny by looking at its states for the 48 characters in MCGINLEY's (1986) data matrix. As expected, *L. aegyptiellum* falls within the *leucozonium* group (Fig. 6) based upon the synapomorphy of long male mandibles (a character which varies homoplastically elsewhere among New World species).

As both *L. leucozonium* (ATWOOD, 1933; STOCKHERT, 1933; PACKER, unpublished observations) and *L. zomulum* (STOCKHERT, 1933; KNERER & ATWOOD, 1962; PACKER,

TABLE 3. — Data from a nest of *Lasioglossum aegyptiellum*. *: mandible wear is scored from 0 (unworn) to 6 (worn down to below the subapical tooth), wing wear is scored as the number of nicks in the wing margin, "tattered" refers to the entire margin being abraded, "very tattered" refers to the entire margin worn away such that wing length cannot be recorded.

Female	Head width (mm)	Wing length (mm)	Degree of abrasion of*	
			Mandible	Wing
1	2.8	6.9	5	tattered
2	2.7	6.5	3	10
3	2.7	6.6	3	tattered
4	2.7	?	2	very tattered
5	2.6	6.1	5	tattered

unpublished observations) are solitary, as are all other *Lasioglossum s.str.* for which data are available (YANEGA, 1997), it is clear that eusociality in *L. aegyptiellum* is a derived condition (Fig. 6).

Taxonomic sampling and Evylaeus. PACKER (1991) provided a phylogeny of eight species of the subgenus *Evylaeus* based upon electrophoretic data. Only one of the included species was known to be solitary and, at that time, another was known to exhibit behavioral polymorphism. The results were unambiguous in demonstrating that the polymorphic species represented a recent reversal to solitary behavior in a montane population in Japan (SAKAGAMI & MUNAKATA, 1972). Whether solitary or eusocial behavior was ancestral to the subgenus as a whole remained

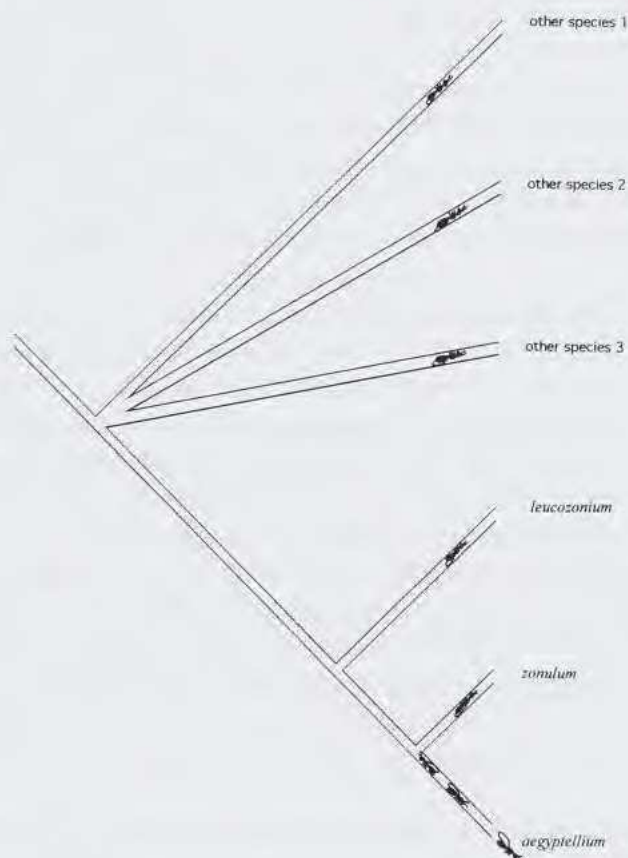


FIG. 6. — Phylogeny for three species in the *leucozonium* group of the genus *Lasioglossum* demonstrating that *L. aegyptellum* has recently evolved sociality. Data from MCGINLEY (1986) with additional information for *L. aegyptellum* which has identical character states to those of *L. zomulum* for all characters used by MCGINLEY that could be assigned character states unambiguously.

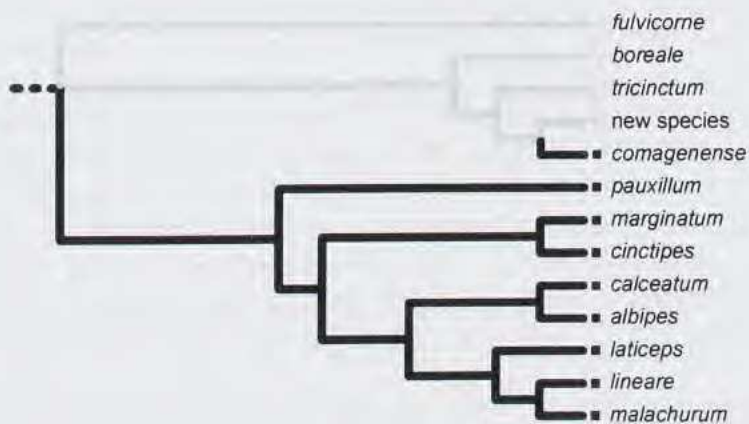


FIG. 7. — Phylogeny for some species of the subgenus *Evyllaes* based upon a total evidence analysis (redrawn from TAYLOR, 1994). For cladogram shading refer to legend for figure 3.

undetermined, partly because the outgroup contained both solitary and social species. Note that the fact that only one purely solitary species could be included in the analysis biased the result in favor of finding that eusociality is ancestral: with only one solitary species in the ingroup and ambiguity as to the outgroup condition it is not possible to optimize solitary behavior as ancestral, this indicates the importance of taxon sampling when incomplete phylogenies and behavioral information are available. Inclusion of the behavioral data into the data matrix used in phylogenetic analysis made no difference to the tree topology although CI and RI were reduced (PACKER, unpublished).

In order to resolve this situation additional information was required for taxa close to the root of the tree. Several North American species are allied with *L. (E.) fulvicorne* (SVENSSON *et al.*, 1977) and so some of these (and other species) were sampled and added to the phylogeny by TAYLOR (1994). In this case the results differ depending upon whether the behavioral data are used in tree construction or not. The behavioral data considered appropriate to include in the phylogenetic data matrix are those that do not vary within species. Thus, whether queen and worker size distributions overlap or not, whether fewer than one percent of the workers mate or not and three nest architectural variables were included whereas solitary versus eusocial behavior, multiple foundress associations and the number of worker broods were not included as these three features are attributes which vary within taxa. One species (*L. (E.) cinctipes*) changes position between electrophoretic and total evidence analyses. The latter approach is preferred both philosophically (KLUGE & WOLF, 1993) and empirically: total evidence places this taxon in a more reasonable position as judged by synapomorphies of the male genitalia (PACKER, unpublished data).

Four equally parsimonious trees were obtained with the total evidence data set with lengths of 125, CI of 0.84 and RI of 0.77. One round of successive approximations character weighting reduced the number of trees to three and the tree statistics stabilized at the second round to a length of 850, CI of 0.94 and RI of 0.92. The resulting Nelson consensus tree is shown in figure 7.

Mapping behavior onto the total evidence phylogeny (Fig. 7) leads to the following conclusions: i) Solitary behavior is ancestral in *Evyllaesus* with eusociality arising in the *pauillum/malachurum* clade and also, as delayed eusociality (in which founding females become queens in their second year of life after their first brood daughter(s) overwinter), in the lineage leading to *comagenense*. ii) Social polymorphism is ancestral to the *albipes/calceatum* species pair (see PLATEAUX-QUÉNU, 1989, 1993 for data on the former species), (social polymorphism – with delayed eusociality and solitary behavior is also known from *comagenense* and its sibling species *L. (E.) fratellum* (VON DER HEIDE, 1992; FIELD, 1996)). iii) It remains probable that the perennial societies of *L. marginatum* are derived from an annually eusocial ancestral condition. However, given the increasing documentation of delayed eusociality (a phenomenon which requires unusually detailed field work). This last conclusion may need to be revised. This is because delayed eusociality is clearly a likely intermediate condition between annual and perennial colony cycles and it seems to occur, at least as a polymorphic attribute, fairly commonly.

As there are many more species in this subgenus that remain unknown behaviorally, a more broadly based phylogenetic study is required. Once a more complete phylogeny including more of the taxonomic diversity in *Evyllaesus* is available, it should be possible to predict which taxa

should be studied in the field in order to narrow down more closely the precise phylogenetic position of the origins of eusociality in these bees.

The genus Dialictus. Many species in this subgenus are known to be social and many solitary (PACKER, 1992, 1994; WCISLO *et al.*, 1993). These small bees are morphologically monotonous and very difficult to identify, let alone analyze phylogenetically. Nonetheless, molecular approaches to *Dialictus* phylogeny are underway (DANFORTH, personal communication). At present, it is not possible to say anything about the phylogenetic interrelationships among those *Dialictus* species whose behavior has been studied. Nonetheless, it appears highly likely that recent transitions from solitary to eusocial behavior (as well as the reverse) can be documented within *Dialictus*.

The genera Augochlorella and Augochlora. A recent phylogeny of genera of the tribe Augochlorini demonstrates that the genera containing eusocial species form a monophyletic clade (Fig. 8; DANFORTH & EICKWORT, 1997). *Augochlorella* is the sister group to the remaining genera and one of its species, *A. striata*, is behaviorally polymorphic at the northern edge of its range (PACKER *et al.*, 1989; PACKER, 1990) but only eusocial further south in New York (MUELLER, 1991) and Kansas (ORDWAY, 1966). As i) the Augochlorini are largely tropical American, ii) only 3 genera reach temperate North America, iii) *A. striata* achieves a higher latitude than any other species and iv) other species of *Augochlorella* are eusocial (YANEGA,

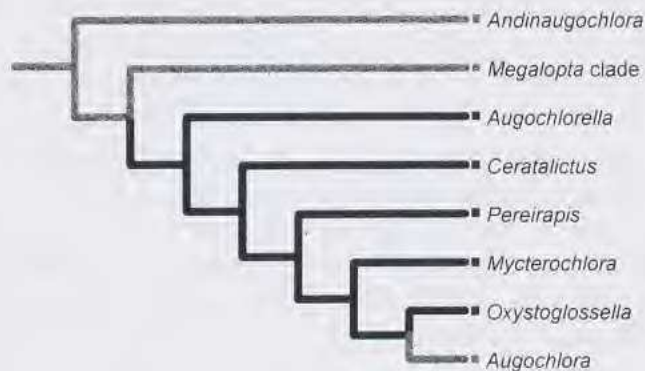


FIG. 8. — Phylogeny of genera of augochlorine bees (redrawn from DANFORTH & EICKWORT, 1997). For cladogram shading, refer to legend for figure 3. Note that for simplicity a clade of eight genera/subgenera, the sister group to the lineage containing the eusocial taxa, is replaced here simply by the "Megalopta clade". Also, there are an additional 13 genera/subgenera more basal to the portion of the phylogeny shown here. Redrawn from DANFORTH & EICKWORT (1997).

1997), it seems safe to assume that the solitary aspect of this locally polymorphic species is the derived condition and is presumably the result of the short summers experienced at the northern latitude on the edge of the species' range (PACKER, 1990).

The subgenus *Augochlora* includes the solitary wood-nesting *A. pura* (STOCKHAMMER, 1966). It is clearly nested well within the eusocial clade of augochlorines and thus is an example of the loss of eusociality.

DISCUSSION

It is now no longer acceptable to make statements concerning the pattern of evolution in some characteristic of interest without reference to a phylogeny that corroborates that pattern (GRANDCOLAS *et al.*, 1994). It is also clear that the incorporation of phylogenetic tests of the polarity of evolutionary change in specific characters often overturns dearly held convictions based upon *a priori* common sense biological "knowledge". This paradigm shift influences not only classifications (the original arena for the application of phylogenetic results) but also evolutionary scenarios.

Cladistic methods provide a means of testing hypotheses of character evolution. If the results indicate that the direction of evolutionary change in the character of interest differs from that traditionally held, then a lot of effort which would have been misdirected can be refocused and events which actually happened can be investigated, rather than patterns which arose only as a result of the preconceived notions of biologists. However, the utility of phylogenetics goes much further than this. Particularly for the more speciose groups of organisms, basic biological data are generally not available for all species yet the sparse information that does exist can be placed within a phylogenetic framework. If a phylogenetic analysis includes taxa for which information on the feature of interest is not available, the results may indicate clearly which taxa occupy crucial transitional positions in the phylogeny and are thereby those which should be studied in the field. If both phylogenetic and behavioral/ecological information are fairly complete, then mapping the traits of interest onto the phylogeny will permit the pattern of evolutionary change(s) in the characteristic of interest to be discovered. Thus, in addition to aiding in the interpretation of field research, through the establishment of polarity, phylogenetics can help us frame testable hypotheses as to how evolutionary changes took place and, through resolution of important areas of the cladogram, suggest to us which species are deserving of further study. Thus, I would argue that phylogenetics is even more fundamental to many areas of biology than is statistics: whereas statistics can tell us how to design experiments and analyze their results, phylogenetics can tell us precisely what changes have occurred in evolutionary history and which characteristics in which organisms are worthy of further study in the field or laboratory.

In this paper I have plotted evolutionary changes between the character states "solitary" and "eusocial" for all groups of Halictine bees for which suitable information is available. For the 6 genera/subgenera studied (no phylogeny is available for *Dialictus*), the solitary species are clearly derived from eusocial ancestors for four of them (*Halictus*, *Seladonia*, *Augochlorella*, *Augochlora*). There are four behaviorally polymorphic species known from among these taxa (Table 2) and for each of them, solitary behavior is likely the recent evolutionary innovation. Thus, with respect to my first question: "what are we studying?" any comparison of solitary and eusocial behavior within polymorphic species or between monomorphic species in these four genera would be analyzing those factors that promote solitary behavior.

In *Evylaeus* all the primarily or purely eusocial species included here share eusociality from a common ancestor. This represents a switch from solitary to eusocial behavior within *Evylaeus*, although the number of species derived from the social common ancestor is quite large.

Phylogenetic study of this subgenus also indicates that two of the behaviorally polymorphic species have solitary behavior as the recent evolutionary innovation. The remaining change to eusociality in *Evyllaesus* occurs in the *comagenense/fratellum* species pair, both of which are behaviorally polymorphic within single populations which exhibit solitary, semisocial and delayed eusocial behaviors (VON DER HEIDE, 1992; FIELD, 1996). This is probably a comparatively recent evolutionary change. Thus, comparisons among *comagenense*, *fratellum* and their solitary relatives could address the question of origins of delayed eusociality. In the genus *Lasioglossum*, the only known eusocial species represents a recent evolutionary origin of eusociality.

Thus, with respect to my second question "what should we be studying?" the following research directions are suggested. First, phylogenetic and behavioral studies of additional species in the *L. leucozonium* group would be desirable. Secondly, further phylogenetic and behavioral studies of relatively basal lineages within *Evyllaesus* would be useful. Thirdly, phylogenetic analysis of behaviorally known *Dialictus* species may be particularly important. Furthermore, if research on the origins of eusociality is to be done, the genera *Halictus* and *Seladonia*, and the tribe Augochlorini (and vespine wasps, apine bees and ants) are best ignored.

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